VEGETATION

OF THE

NORTH HAVEN SAND PLAINS

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(WITH PLATES 23–28)

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PART I: PHYSIOGRAPHY AND VEGETATION

BRIEF DESCRIPTION OF THE REGION

Stretching northward along the east side of the Quinnipiac River valley for fifteen or sixteen miles, almost the entire distance from New Haven to Meriden, Connecticut, is a narrow sand plain or series of sand plains. Though perhaps once continuous, the area is now crossed by small streams which have cut their channels through the sand. In some instances alluvium has been formed along the beds of these streams supporting a somewhat different class of plants than is found on the plains. In this way the area is divided transversely into a number of small plains.

A large portion of this land has been improved, is now cultivated and produces fair agricultural crops. Some of the factories of Wallingford are built upon this land, as are also portions of the villages of North Haven and Montowese. Many acres, however, may be called waste land and are covered only with red cedars and *Andropogon scoparius*. The Hartford division of the New York, New Haven and Hartford railroad crosses this area longitudinally from North Haven to its northern extremity near Meriden, and the Air Line division of the same railroad crosses the southern end obliquely at Montowese.

Over nearly the entire region we find here and there certain small tracts, resembling miniature deserts, where the conditions have not been favorable for plant growth and which are quite barren. Why should such small areas remain still practically uncovered by vegetation? The answer must be found in the unfavorable character of the soil, which will later be described briefly in this paper. In the opinion of the writer, a much greater portion of the sand plains was formerly barren, and two facts support this opinion: (1) There are no evidences that the plains were ever covered with forest growth; no large trees remain and, if such had ever existed and were removed, there would be sprouts or stumps to tell the story, for stumps do not decay rapidly in such a soil. (2) The areas are now being gradually covered through the agency of certain plants that are able to grow under the conditions that prevail upon these sand plains.*

The present paper is an account of observations on the flora of these barren areas, and of the result of examinations of the structure of certain of these plants to ascertain if they show any special adaptations that enable them better to meet the conditions found in such situations. For the purpose of the investigation two barren areas were chosen because they were among the largest of these sterile tracts, and more accessible to the writer than were the other similar areas. One of these is an irregular-shaped area of perhaps eighty or ninety acres situated a short distance north of the village of North Haven, and is the region that will be referred to as the North Haven tract. A smaller area

* Since this was written, the writer has been assured that the barren areas were formerly much larger and are being gradually covered by vegetation.

containing nearly forty acres, near the Montowese station of the Air Line division of the New York, New Haven and Hartford railroad, was also studied and will be designated the Montowese tract.

These tracts are about three miles apart, being separated by land of similar formation and character which has been improved and is now used for tillage and for pasture. The Montowese tract is bordered on the west by the Quinnipiac River, but is several feet higher than the water in the river. The topographical lines on the map of this region prepared by the United States Geological Survey show the Montowese tract to be about twenty feet above sea-level and the North Haven tract to be not far from forty feet.

The writer had often noticed these sand barrens from railway trains and first in May, 1899, was able to reach them for a day's collecting. In the spring of 1901 it was decided to make a somewhat systematic study of the plants of this region and from April to October of this and the following year (1902) each tract was visited about once in two weeks and the flowering plants collected and field notes made about the flora of the region. Specimens were pressed and mounted, and the roots of many species were preserved in formaldehyde solution for histological study.

It must not be inferred that the boundaries of these areas are naturally well-defined, for except where the river washes away the sand from the Montowese tract the soil-formation is much the same without as within the boundaries of the areas. But it is more densely covered with vegetation, though producing the same species of plants, showing that in some respects at least, the conditions must have been more favorable for plant growth than on the barren areas. In fact these areas may fairly be regarded as the least favorable, as they are the last to be covered with vegetation.

Winds and water have changed slightly the topography of both tracts, but as they are not particularly exposed, the winds do not have a very long sweep and the shifting of the sand is not rapid. That it exists, however, observation is the only proof required. Some of the trees have their roots laid bare by the winds, where the ground is so nearly level as wholly to preclude the idea of washing (see *pl. 25, b*). A board fence along the west side of the railroad track at Montowese (also shown in *pl. 25, b*), con-

structed for the purpose of keeping either sand or snow from blowing upon the tracks, is banked on its west side by a sand drift of half its height. Here the west winds are chiefly instrumental in the shifting, and on the bank of the river much of the finer sand has been removed by it. Slight shifting by winds also occurs on the North Haven tract. Heavy showers, upon the sand where the ground is not perfectly level, cause temporary erosion, by the surface water on its way to lower levels washing away the sand in its path. At Montowese such water goes into the river, but the preparation of the railroad-bed across the North Haven tract necessitated some cutting and filling and excavations were made in the sand for filling material. These excavations give the surface waters a chance to reach a lower level and channels are cut in the sand. In a clay formation such channels are deep with steep banks but in loose sand they are very shallow with widely sloping banks because the soil particles will not hold together. On the banks the winds also strike with greater force than on the level and several trees are left with exposed roots from the combined effect of winds and washing away of the sand (see *pl. 25, c*).

SOIL AND MOISTURE

It has already been mentioned that edaphic factors (*i. e.*, soil conditions) are chiefly responsible for the barren state of these areas. The soil is mostly sand of medium fineness, or gravel containing pebbles, an inch or so in diameter in some places, of which broken red sandstone forms a part. This formation is called drift and is of glacial origin. It is probably the deposit of the water from the melting glacier and not the moraine. No chemical analyses were made to determine the fertility of the soil of these desert regions, but during the seasons of 1898 and 1899 the Connecticut Agricultural Experiment Station conducted some experiments with forage plants near the Montowese railroad station only a short distance from the barren area. The ground used in the tests had formerly been cultivated, but was neglected for many years, and the soil contained only .09 of one per cent. of nitrogen. It is probable that this soil also has small quantities of phosphoric acid and potash as is the case with other similar soils. But as leguminous plants are able to obtain nitrogen from the air, these

might be expected to grow here, were a lack of soil fertility the only handicap. What seems to be a more important factor is the almost total absence of humus or organic matter. Whitford records the existence of similar conditions on the sand beaches of northern Michigan,* and observes that such a soil is favorable for the development of creeping stems and rhizomes.

Though the sand appears to be dry at the surface I have always found plenty of moisture a few inches below the surface, even in a protracted drought. The explanation may be found, perhaps, in the low altitude of the region and its proximity to tide-water. The North Haven tract is only about forty feet above tide-water and less than three miles from it, as the tide sets back quite a distance from the mouth of the Quinnipiac River. The Montowese tract is less than twenty feet above the tide-water, which reaches to its very edge. The mechanical condition of the soil enables the moisture to rise quite rapidly to the surface, from a considerable depth, through capillarity.

In order to obtain water for the forage experiments just mentioned a well was driven fifteen feet deep, and the pipe contained water to the height of four feet from the bottom. The well was upon ground higher than the barren area. A considerable excavation has been made beside the railroad a short distance north of the North Haven tract and water stands in this excavation except in a very dry time.

Evaporation must be very great from such a soil and the continual drying up of the surface together with the intense heat on sunny days is probably the excuse for the scanty vegetation of the region. Thousands of seedlings must perish each season by drying up before the roots gain a sufficient depth to provide the necessary moisture. In several cases heavy wagons had crossed the sand and the sunken tracks were filled with young seedlings of *Trichostema dichotomum*. These seedlings had grown so much larger and closer together than those outside the tracks, that they could be seen for some distance as green lines or ribbons stretched across the plains. The sand was here compressed two or three inches below the surrounding level and the germinating seeds found

* Whitford, H. N. Genetic development of the forests of northern Michigan; a study in physiographic ecology. Bot. Gaz. 31: 289–325, *f. 1–18*. 1901. (Page 298.)

a more abundant moisture supply as well as a firmer foothold. Doubtless many of the seeds were blown into the furrows. Annual plants must usually mature before the hot days of July and August or they perish without perpetuating the species.

No records were made of the temperature of the soil or of the atmosphere near the soil, but unquestionably both would be several degrees higher near the surface than where the soil is covered with turf, or where the soil is of a different character.

The rainfall on these areas is probably not very different from the official record of the Weather Bureau at New Haven. The record of the rainfall as well as the temperature by months for the two years during which these studies were made is here given:

PRECIPITATION

	1901	1902
January,	1.38 inches.	1.83 inches.
February,	.54 "	3.58 "
March,	5.80 "	4.63 "
April,	9.03 "	3.40 "
May,	6.38 "	1.61 "
June,	.25 "	4.35 "
July,	4.40 "	3.26 "
August,	6.92 "	2.14 "
September,	5.70 "	5.84 "
October,	2.95 "	6.41 "
November,	1.61 "	.79 "
December,	7.65 "	6.49 "
Total,	52.61 inches.	44.33 inches.

TEMPERATURE

	1901			1902		
	Mean	Maximum	Minimum	Mean	Maximum	Minimum
January,	28	49	— 1	27	49	6
February,	24	41	8	27	50	11
March,	36	52	9	42	65	22
April,	47	69	35	47	80	32
May,	55	80	39	57	85	36
June,	68	94	47	64	89	47
July,	74	97	53	69	90	53
August,	72	86	56	68	87	52
September,	64	87	41	63	84	45
October,	53	76	31	53	74	31
November,	37	60	12	46	67	26
December,	31	59	5	28	53	— 5
	49	97	— 1	49	90	— 5

During 1901 annual vegetation was scarce on the sand plains, but it was much more abundant during 1902. The only explanation can be found by looking up the record of rainfall for June, which in 1901 was only .25 inch, while in 1902 it was 4.35 inches. More rain fell in May and July of 1901 than came in the corresponding months of 1902, but June is the month when most annuals appear on the plains and the amount of rainfall for that month is therefore a criterion of the abundance of annual plants for the season.

VEGETATION

The chief forms of vegetation of this region are essentially xerophytic in character, though the conditions under which they are produced may not be strictly xerophytic. No great lack of moisture exists, but the burning heat of the sun on the sand enables only xerophytes to persist; other plants perish soon after the seeds germinate.

Andropogon scoparius grows in tufts on both the North Haven and Montowese tracts (see *pl. 23, a*) and is probably the most abundant of all the perennial grasses. A single patch of *Andropogon furcatus* occurs at North Haven. This plant has thickened root nodes (see *pl. 27, e*) in which food and moisture are stored up and carried through the winter. On both tracts *Cyperus filiculmis* is the most common sedge, and the dead and dried tubers may be seen partly uncovered in many places where the plants have been killed through fire or some other agency. In the clumps of trees *Poa compressa* is found sparingly. During 1902 an annual grass came up very abundantly on the sand at Montowese during the latter part of June and was probably the most abundant annual of the region, forming a thick carpet in many places. This proved to be *Sporobolus vaginaeflorus*, and in company with it occurred *Syntherisma sanguinalis* and *S. filiformis*, both being annuals. Other common annuals growing here were blue curls (*Trichostema dichotomum*), which was the most abundant annual plant on the North Haven tract, and *Polygonella articulata* common to both areas. *Sarothra gentianoides* (*Hypericum nudicaule*) was common at North Haven, where during both seasons this little plant formed green patches upon the sand (see *pl. 25, a*). Among the perennial herbaceous dicotyledonous plants the milk-

weeds (*Asclepias Syriaca*, *A. amplexicaulis* and *A. verticillata*), *Lespedeza*, *Baptisia tinctoria*, *Meibomia*, *Helianthemum majus* and *Artemisia caudata* predominate. *Rubus procumbens* (*R. Canadensis* of authors) is also abundant, covering the ground in many places. At North Haven it grows in the grass (*Andropogon scoparius*) around the boundaries of the barren area, but at Montowese it grows and fruits heavily on the bare sand. The red cedar (*Juniperus Virginiana*) is the most common conifer of the region, though *J. communis* occurs frequently and a notably large specimen growing at Montowese is about thirty feet in diameter.

Many black cherry trees (*Prunus serotina*) are found around the margins of the Montowese tract, and there are several sassafras trees. The latter have a tendency to form colonies by sprouting from the roots. The common milkweed (*Asclepias Syriaca*) also occurs in colonies, one of which is shown on *pl. 24, b*. *Baptisia tinctoria* is abundant at Montowese and is shown on *pl. 23, b*.

A peculiar feature of the sand plains is the total absence of cruciferous plants. Certain species like *Lepidium Virginicum* and *Bursa Bursa-pastoris* are commonly found in similar places. No cruciferous plants were found on either tract during the two seasons that plants were collected. Then, too, certain plants of the pink family (Caryophyllaceae) like *Arenaria* and *Tissa* and the chickweeds might fairly be expected to grow in such places. The pink family is represented only by soapwort or bouncing bet (*Saponaria officinalis*), which occurs on the North Haven tract.

One very interesting feature of that portion of the North Haven tract lying west of the railroad, is the presence of numerous scrubby black oaks (*Quercus velutina* = *Q. coccinea tinctoria*) scattered about over the region (*pl. 24, a*). Two questions suggest themselves simultaneously — (1) Why does the black oak grow here instead of other trees? (2) Why are the oaks so scattered instead of occurring in groups? From a careful study it seems to the writer that the acorns which produced these trees must have been buried in the sand either by squirrels or by some other agency, for those that now fall upon the surface of the ground each year from the parent trees never making seedlings. At least, probably not one in a thousand ever does. They fall upon

the sand under the trees, probably germinate and dry up before the radicles can reach a sufficient depth to obtain the necessary moisture. In some unpublished investigations Professor J. W. Toumey has found that in hard soil the radicle is not able to work its way into the soil, but on account of the lightness of the acorn it is tumbled about on the surface. The shells form a coating on the sand under the oaks, and with fallen leaves and other waste vegetable matter that is blown about, help to form a thin layer of leaf-mold where not destroyed by fire.

Under these oaks grows a moss, *Polytrichum piliferum*, which also aids in the formation of soil. The rhizoids hold together the upper two inches of sand, thus preventing it from shifting, and the plant doubtless has some influence on the retention of the moisture. Therefore certain plants grow in company with the moss which do not appear on other portions of the sand area and which probably could not persist there. The scrub-oak (*Quercus nana*) also grows at North Haven and there are several specimens of dwarfed chestnut trees.

Certain areas on the North Haven tract are covered with reindeer moss, *Cladonia rangiferina*, and where this lichen becomes established other plants soon spring up. It holds the sand from shifting, and leaves and other portions of plants blown about by the winds finally lodge upon it creating a thin layer of slowly decaying vegetable matter. The surface being undisturbed and the leaf-mold retaining a portion of the moisture that formerly escaped through evaporation, seeds that fall upon this area are able to germinate and grow. Sweet fern (*Comptonia peregrina*) covers quite an area near the reindeer moss and may perhaps follow it as the next stage in the development of a forest growth on this land.

Much of the accumulating humus on the North Haven tract has been destroyed by fires probably started by sparks emitted from passing engines. Leaves and dry grass have been burned in this manner and in one locality the sedges collected show the result of such fires; the old culms had been burned off level with the sand and from the blackened base the new growth had been pushed out. Fires cannot sweep over the whole area for lack of combustible material, yet the dry leaves which have lodged be-

tween the stems of grasses and other plants covering small areas here and there are frequently burned off in this manner, thus destroying small quantities of what is most needed to make this a plant-producing soil — humus, or organic matter.

Though certain species of plants must necessarily remain constant in this region, the flora doubtless changes somewhat from year to year, and if these studies should be continued several new plants would probably be found, while some of the plants collected might disappear.

A feature to be noted is the presence of several plants commonly found in swampy regions. *Rhus radicans* forms large masses of foliage at North Haven and though common throughout Connecticut, grows often in swamps in northern New England. *Nyssa sylvatica* and willows are swamp trees, and *Spartina cynosuroides* is common to the brackish marshes of the coast.* *Aronia* (or *Pyrus*) *arbutifolia* is a denizen of wet places as are *Vaccinium corymbosum* and *Kalmia angustifolia*, all growing in shallow water in many swamps. *Ilex verticillata* is also an inhabitant of damp ground. *Stenophyllus* (or *Fimbristylis*) *capillaris* and *Rosa Carolina* are also found in moist places.

Following is a list of the chief plants of the region collected during 1901 and 1902, with the exception of a few specimens gathered in 1899. All were found growing within the limits of the regions, except *Lupinus perennis*, which grows in large areas a short distance north of the North Haven tract, and *Cracca Virginiana*, which covers quite a plot of ground a few rods southwest of the Montowese tract. The latter is also a common inhabitant of the sand plains through Wallingford and is found just north of the limits of the North Haven tract. These two plants have been included because they are important plants for the region and occur on the same formation and under practically the same conditions, though not actually found growing within the arbitrary limits of our tracts.

The nomenclature is that used in Britton's Manual, the name used in Gray's Manual, sixth edition, being cited in parentheses when different.

* Winton, A. L. Forage plants of the salt marshes of Connecticut. Conn. Agric. Exp. Sta. Ann. Rep. 1889: 233–245. 1890.

LIST OF THE MORE IMPORTANT PLANTS

In all 135 species of plants were collected on the sand plains in 1901 and 1902. Many of these were rare and of no importance in covering the sand. The species here given are some of the more abundant ones:

Juniperus communis L. Frequent, occurring on both tracts.

Juniperus Virginiana L. Common at both North Haven and Montowese, the most abundant of all Coniferae.

Andropogon scoparius Michx. The most common perennial grass of the plains, forming tufts. Grows at both North Haven and Montowese, and is to be considered an important factor in covering the soil.

Andropogon furcatus Muhl. A single patch several feet in diameter grows at North Haven east of railroad. This species is larger than the preceding and spreads by rootstocks.

Syntherisma sanguinalis (L.) Dulac. (*Panicum sanguinale.*) Frequent at Montowese.

Panicum depauperatum Muhl. Occasional at North Haven, forming low tufts on the sand.

Sporobolus vaginaeflorus (Torr.) Wood. Extremely abundant at Montowese in 1902, much less so in 1901. Grows very quickly.

Spartina cynosuroides (L.) Willd. Occasional in several places on bank of Quinnipiac River at Montowese.

Poa compressa L. Frequent, especially around trees at North Haven and Montowese.

Cyperus filiculmis Vahl. The most common sedge at both places, growing in loose tufts on the sand.

Stenophyllus capillaris (L.) Britton. (*Fimbristylis capillaris.*) Frequent at both places.

Carex Pennsylvanica Lam. Occurs west of railroad, near ravine, North Haven tract.

Carex Muhlenbergii Schk. Occasional at both places.

Populus grandidentata Michx. Frequent at North Haven and Montowese.

Comptonia peregrina (L.) Coulter. (*Myrica asplenifolia.*) Common, forming large patches at North Haven.

Betula lenta L. Frequent, North Haven tract.

Betula populifolia Marsh. Common.

Castanea dentata (Marsh.) Borkh. (*C. sativa Americana*.) Common in both places.

Quercus velutina Lam. (*Q. coccinea tinctoria*.) The commonest tree on the North Haven area, and is common at Montowese.

Quercus palustris Du Roi. Frequent at North Haven and Montowese.

Quercus nana (Marsh.) Sarg. (*Q. ilicifolia*.) Occasional. Several plants at North Haven.

Rumex Acetosella L. Common on both areas.

Polygonum Convolvulus L. Rare. Occurs at North Haven.

Polygonella articulata (L.) Meisn. Common in late summer at North Haven and Montowese.

Liriodendron Tulipifera L. Three or four trees occur east of railroad at North Haven.

Thalictrum purpurascens L. Frequent on edge of Montowese tract.

Berberis vulgaris L. Occasional.

Sassafras Sassafras (L.) Karst. (*S. officinale*.) Frequent at North Haven and Montowese. At Montowese several large trees have sprouted from the roots, forming groups of small trees.

Platanus occidentalis L. A few trees at North Haven.

Amelanchier Canadensis (L.) Medic. Frequent, several dwarfed specimens at North Haven.

Rubus procumbens Muhl. (*R. Canadensis* of Gray's Manual.) Common on both areas, and covers the ground in places; grows with *Andropogon scoparius*.

Fragaria Virginiana Duchesne. Common on both tracts.

Potentilla Canadensis L. Common.

Prunus Virginiana L. Occurs at North Haven.

Prunus serotina Ehrh. Common in both places.

Baptisia tinctoria (L.) R. Br. Common. The most common perennial legume at Montowese (see *pl. 23, b*). Rather rare at North Haven on the barren area, but occurs around it and farther north.

Crotalaria sagittalis L. Frequent, growing along the sides of the railroad, in company with *Strophostyles helvola*.

Lupinus perennis L. Does not occur within the limits of either the North Haven or Montowese tracts, but grows in abun-

dance in fields northeast of the former, covering many square rods. Also occurs northeast of the Montowese barren area.

Cracca Virginiana L. (*Tephrosia Virginiana.*) Like *Lupinus perennis*, this plant does not belong strictly within the limits of our area, but grows in great abundance just south and west of the Montowese plain. It is also common north of the area studied at North Haven and is a very important plant for such regions.

Robinia Pseudacacia L. Common at North Haven where there are several medium-sized trees.

Meibomia Dillenii (Darl.) Kuntze. (*Desmodium Dillenii.*) Frequent. Grows near railroad at North Haven.

Meibomia Canadensis (L.) Kuntze. (*Desmodium Canadense.*) Common, both at North Haven and at Montowese.

Lespedeza capitata Michx. Common on both areas.

Strophostyles helvola (L.) Britton. (*S. angulosa.*) Common at both places along the railroad tracks.

Euphorbia polygonifolia L. Occasional at Montowese near river.

Rhus radicans L. Common in both places forming dense, low, foliage masses and covering the ground around the bases of trees. An important xerophyte.

Rhus glabra L. Frequent.

Rhus hirta (L.) Sudw. (*R. typhina.*) Occurs at Montowese near the railroad.

Rhus copallina L. Frequent both at North Haven and at Montowese, growing in the sand with *Rubus procumbens.*

Celastrus scandens L. Common both at North Haven and at Montowese, occurring usually in groups of trees or plants.

Sarothra gentianoides L. (*Hypericum nudicaule.*) Abundant at North Haven, where it formed a carpet over several large areas of sand during midsummer (see *pl. 25, a*). Much more abundant in 1902 than in 1901, probably on account of moisture.

Helianthemum majus (L.) B.S.P. Common on the sand at both places, fruiting heavily.

Viola sagittata Ait. and *Viola pedata* L. Frequent, both at Montowese and at North Haven, the roots being buried deep in the sand in many cases.

Nyssa sylvatica Marsh. Occurs at North Haven east of railroad.

Azalea nudiflora L. (*Rhododendron nudiflorum.*) Two plants stand alone in the sand west of railroad near north end of New Haven tract.

Kalmia angustifolia L. Occurs near north end of North Haven tract west of railroad, around the outside of a clump of bushes.

Gaylussacia resinosa (Ait.) Torr. & Gray. Occurs near north end, west of railroad, North Haven tract.

Vaccinium corymbosum L. Several large plants west of railroad, north end of North Haven tract.

Lysimachia quadrifolia L. Frequent on both areas growing around or in shade of the clumps of trees.

Asclepias Syriaca L. (*A. Cornuti.*) Common, especially at Montowese where it grows in colonies. A colony on a mound is shown on *pl. 24, b.* Roots run very deep.

Asclepias amplexicaulis J. E. Smith. (*A. obtusifolia.*) Common on both areas where it is deep-rooted in the sand.

Asclepias verticillata L. The most abundant milkweed of the sand plains, generally growing with grass or weeds, seldom in the open sand.

Trichostema dichotomum L. Common. One of the few annuals abundant on both tracts. Plants usually very small and some even killed before maturing. More abundant in 1902 than in 1901.

Verbascum Thapsus L. Occasional at North Haven.

Linaria Canadensis (L.) Dumont. Common all over the North Haven area. In grass around the barren tract, the ground was blue with the flowers on June 8, 1901.

Linaria Linaria (L.) Karst. (*L. vulgaris.*) Frequent at North Haven.

Chrysopsis falcata (Pursh) Ell. Occurs at south end of North Haven tract west of railroad.

Solidago nemoralis Ait. Frequent.

Ionactis linariifolius (L.) Greene. (*Aster linariifolius.*) Frequent around clumps of trees east of railroad at North Haven.

Leptilon Canadense (L.) Britton. (*Erigeron Canadensis.*) Common in both places.

Erigeron ramosus (Walt.) B.S.P. (*E. strigosus.*) Frequent.

Ambrosia artemisiaefolia L. Common; small plants found on both tracts.

Achillea Millefolium L. Frequent.

Chrysanthemum Leucanthemum L. Frequent.

Artemisia caudata Michx. Common, especially at North Haven, where it grows with *Rubus procumbens* and *Andropogon scoparius.*

PART II: STRUCTURE OF PLANTS EXAMINED

Considerable attention has been given to the structure of the leaves and stems of plants, for it is in them that the most striking modifications have taken place to prevent a loss of moisture through transpiration. The plants of the Arabian desert, between the lower Nile and the Red Sea, have been studied by Volkens, who has published an elaborate work* on this subject in its ecological relations. Schimper figures the structure of certain leaves and stems in his Pflanzen-geographie.† More recently Kearney has recorded the anatomy of the leaves of some of the plants of the North Carolina strand ‡ and explained the ecological significance of the structures. This line of research is carried still farther by the same author in his report on a botanical survey of the Dismal Swamp region.§ In 1899 Mr. Thomas A. O'Brien in manuscript interpreted the structure of *Spartina cynosuroides, Carex Muhlenbergii, Cyperus filiculmis* and *Poa compressa.*¶ But little attention has been paid to the root structures of plants in relation to environment. The roots of many grasses and sedges have been studied by Mr. Theodor Holm, who has

* Volkens, G. Die Flora der aegyptisch-arabischen Wüste. 156 pp. *18 pl.* Berlin, 1887.

† Schimper, A. F. W. Pflanzen-geographie auf physiologischer Grundlage. 876 pp. *502 f. + 4 maps.* Jena, 1898.

‡ Kearney, T. H. The plant covering of Ocracoke Island: a study in the ecology of the North Carolina strand vegetation. Contr. U. S. Nat. Herb. 5: 261–319, *f. 38–50.* 1900.

§ Kearney, T. H. Report on a botanical survey of the Dismal Swamp region. Contr. U. S. Nat. Herb. 5: 321–550, *pl. 66–76 + f. 51–85.* 1901.

¶ O'Brien, T. A. The ecological structure of four native xerophytes. Manuscript presented as a graduating thesis, Sheffield Scientific School of Yale University, 1899.

published a number of papers in the Botanical Gazette * and in the American Journal of Science,† but while the author points out the probable uses of certain structures they are not considered from the ecologist's standpoint.

The present writer has examined the roots of a number of plants found growing upon the sand plains for the purpose of ascertaining to what extent the subterranean parts of the plants become especially adapted for taking up and holding moisture. Any corresponding adaptations of leaves and stems which have come to his notice are considered in the present paper.

A microscopic study has therefore been made of the leaves of twenty-three species, the stems of three, the roots of thirty-five, and the rhizomes of seven.

HISTOLOGY OF LEAVES AND STEMS

The material examined was collected on the sand plains. Leaves of several species were preserved in formaldehyde solution, but in some instances it was necessary to examine dried material which was first soaked in potash-water. All sections were cut by hand.

POLYTRICHUM PILIFERUM. — The central portion of the leaf is more than a single layer of cells in thickness, while the edges of the leaf are formed of a single layer and are rolled upward at the base. The thickened portion bears near the base of the leaf a large number of lamellae. The edges of the leaf roll in such a manner as to cover the lamellae, forming an excellent hindrance to the loss of moisture. The lamellae are doubtless capable of absorbing much water and are not greatly injured if they become dry.

SYNTHERISMA SANGUINALIS. — About four layers of large water-cells are found over the keel, forming more than half the thickness of the leaf (see *pl. 26, e*). The entire epidermal layer is of similar colorless cells and forms about one third of the thickness of the leaf.

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* Holm, T. A study of some anatomical characters of North American Gramineae. Bot. Gaz. **16**: 166–171, *pl. 15*. 219–225, *pl. 21, 22*. 275–281, *pl. 23, 24*. 1891; **17**: 358–362, *pl. 21*. 1892; **20**: 362–365, *pl. 26*. 1895; **21**: 357–360, *pl. 27, 28*. 1896; **22**: 403–406, *pl. 20*. 1896.

† Holm, T. Studies in the Cyperaceae. Am. Jour. Sci. IV. **3**: 121–128, *pl. 4*. 1897; **4**: 13–26, *f. 1–19*. 298–305, *f. 1–4*. 1897; **7**: 171–183, *f. 1–9*. 435–450, *f. 1–14*. 1899; **9**: 355–363, *f. 1, 2*. 1900; **10**: 33–47, *f. i–iii*. 266–284. 1900; **11**: 205–223, *f. 1–3*. 1901; **14**: 57–63, *f. 1–7*. 417–425, *f. 1–11*. 1902.

The lower epidermis is made up of smaller colorless cells. The cells are much enlarged locally around the bases of long, simple unicellular hairs; subepidermal strands of stereome occur on the upper surface as follows: On the outside of the water-holding tissue over the keel and above eight of the largest mestome bundles. Similar strands are found on the under surface at the keel and below a part of the mestome bundles including the larger and some of the smaller ones. The small mestome bundles are each enclosed by a parenchyma sheath showing four or five cells in cross-section. Stomata occur on both surfaces, but are far more abundant on the lower surface.

PANICUM DEPAUPERATUM. — Upper side of leaf deeply grooved between the bundles, with shallow grooves opposite on lower side; also shallow grooves opposite the mestome bundles on the lower surface. Keel is not prominent and its bundle is only slightly larger than the other largest mestome bundles. Bundles are enclosed in a sheath of stereome which is not fully developed in some of the smaller ones, the cells having lamellated and pitted walls. Outside of the stereome sheath is a parenchyma sheath found in connection with all the bundles. The parenchyma-sheath cells are of good size and show no green coloring matter. Two or more cells of the stereome sheath are replaced on the upper side by parenchyma-cells, a tier of which extends from the bundle upward to the subepidermal stereome strand of the ridge of the upper surface. Similar tissue connects the bundle with the subepidermal stereome tissue of the lower surface. A layer of rather thick-walled cells (probably tracheids) separates the hadrome from the leptome in the larger mestome bundles, but in the smaller ones the elements are not clearly differentiated. Subepidermal strands of stereome occur in the leaf-margins and above and below each bundle. The epidermal layer of the upper surface consists of colorless cells, very small over the stereome strands, with large cells in the grooves that probably function as bulliform cells. Inferior epidermal cells are colorless, of medium size between the mestome bundles, but very small over the stereome tissue opposite the bundles. Certain epidermal cells of the ridges of the upper surface are extended into stout, blunt-pointed hairs, and sharp-pointed unicellular hairs are borne in the grooves of both

surfaces. Stomata occur on both surfaces on the sides of the grooves between mestome bundles. Assimilating cells fill the entire space between the epidermal layers and between the bundles.

CENCHRUS TRIBULOIDES.— Over the keel are two or three layers of bulliform cells forming one half the thickness of the leaf. A single layer extends over the upper surface of the leaf, being partially interrupted over the stereome strands. This layer forms nearly one third of the thickness of the leaf. The lower surface has an epidermal layer of smaller colorless cells which undoubtedly serve a similar purpose. The bundles are all enclosed in parenchyma sheaths. Large green cells surround the small mestome bundles, but these cells are considerably smaller in the sheaths of the larger bundles. The small bundles do not have the leptome and hadrome clearly differentiated. Subepidermal strands of stereome occur on the keel and margins of the leaf, and above and below the larger mestome bundles. To some extent the leaf is furrowed on the upper surface, typical bulliform cells occurring in the furrows, and short spines or hairs which are modifications of the epidermal cells appear on the ridges. Stomata are found on the sides of these furrows, but are much more abundant on the lower surface, where they occur in rows between the mestome bundles.

ANDROPOGON SCOPARIUS.— Over the midrib there are nine or ten rows of very large bulliform cells, of pyriform shape in cross-section (shown on *pl. 26, g*). These are a continuation of the epidermis of the upper surface of the leaf which is composed of a layer of water-cells, this layer making fully one third of the thickness of the blade. Outer walls of cells are much thicker than the partition walls between the cells. Over the mestome bundles the cells are smaller and some are extended into stout pointed hairs. Keel formed mostly of stereome-cells. Subepidermal strands of stereome tissue are found above and below the larger mestome bundles. The large bundles are provided with a sheath of stereome-cells, and a row of similar thick-walled cells separating the leptome and hadrome. Small bundles have a sheath of rather thin-walled parenchyma-cells, and are not clearly differentiated into leptome and hadrome. Stomata do not occur on the upper

surface but are found in one or two rows of cells between the nerves of the lower surface. The guard-cells of the stomata are very narrow and have thick walls with the lumina nearly closed.

ANDROPOGON FURCATUS.— Superior surface covered by a layer of large colorless parenchyma or bulliform cells. Over the larger mestome bundles these cells are very small or the layer is interrupted entirely. Cells of the inferior surface are also colorless but much smaller than those of the upper surface. On both surfaces, especially over the mestome bundles, certain cells are extended into short, stout, unicellular hairs. Subepidermal strands of stereome occur opposite the larger mestome bundles on both the upper and lower surfaces; small strands occur below nearly all of the smaller mestome bundles. The keel is chiefly composed of stereome-cells having very thick walls, in many cases almost obliterating the cell lumina. A small strand of stereome occurs on the upper side of the midrib and on each side of this strand are situated several rows of large bulliform cells. Each small mestome bundle is surrounded by a sheath of large parenchyma-cells from which radiates a row of green palisade-cells connected between the bundles with cells of similar tissue. Bundle of midrib nearly enclosed by sheath of parenchyma-cells, supplemented by cells of stereome on the leptome side. Leptome and hadrome separated by a row of thick-walled cells, which are probably tracheids. Elements are not clearly differentiated in the small mestome bundles. Stomata are abundant in the grooves of the inferior surface.

SPOROBOLUS VAGINAEFLORUS.— Rolls into a cylinder on drying. A group of five (one very large and four smaller) bulliform cells occur between the mestome bundles on the superior surface. A similar arrangement is found on the under surface, though the cells are smaller. Larger mestome bundles are each provided with a sheath of colorless parenchyma-cells and all bundles have sheaths of large, greenish-yellow parenchyma-cells with rather thick walls. Above and below each mestome bundle occurs a strand of stereome tissue, the one on the lower side being much broader than the one on the upper side. In some of the larger bundles having a stereome sheath the parenchyma sheath is interrupted next to the stereome strands, the interruption occurring

more frequently on the leptome side. In some cases a single large colorless cell completes the connection. Epidermal cells are very small over stereome tissue and some of them are extended into spiny or hair-like projections which overhang the grooves, protecting both the stomata and the bulliform cells, and occurring on both superior and inferior surfaces. In the grooves of the inferior surface there are curious unicellular projections showing cell-contents and resembling glandular hairs. The spiny projections of the epidermal cells appear to be empty. Stomata occur along the sides of the bulliform cells on the upper surface and in the grooves of the lower surface. Mesophyl borders directly on the larger cells of the sheath and also upon the bulliform cells.

POA COMPRESSA. — Leaf is conduplicate on drying. Sections examined have large bundle in keel and seven mestome bundles on each side. Subepidermal strands of stereome occur in the keel, in the margins of the leaf, and opposite most of the mestome bundles on both the upper and lower surfaces, though not arranged regularly. In some cases these stereome strands connect the bundles with the epidermis. Epidermal cells of the upper surface have their inner walls in the same plane, but the outer extremities are very irregular. On each side of the keel the epidermal cells are greatly enlarged, and probably serve for storing water. Epidermal cells of the upper surface have the outer walls much thickened, which is not the case with the cells of the lower surface. The cells of the lower epidermis are quite uniform on their outer surface and have thin walls. The small mestome bundles are each provided with a parenchyma sheath; the larger bundles have a sheath of stereome inside the parenchyma sheath. Stomata are found on both surfaces; in slight depressions on the lower surface and in modified depressions of the upper surface, forming grooves * of nearly the depth of the thickness of the epidermal layer of cells. This layer is connected with the guard-cells of the stomata by very small cells which are doubtless modifications of the epidermal cells. Stomata of the lower surface are much larger than those of the upper surface. Stout blunt hairs or spines occur along the keel and the margins, and sharp-pointed ones are found on the upper surface opposite some of the mestome bundles.

* O'Brien, MSS. (see fifth footnote on p. 585).

BROMUS TECTORUM. — Epidermal layers of the two surfaces are very similar, the cells being perhaps slightly larger below, of medium size and colorless. Some of them are extended into long, unbranched, unicellular hairs, which are slightly longer on the upper than on the lower surface. The small mestome bundles are not enclosed in sheaths as in *Cenchrus* and *Spartina*. The larger bundles have parenchyma sheaths, but the cells are small. Subepidermal strands of stereome are found in the leaf-margins and above and below the larger mestome bundles including the bundle of the keel. Mesophyl is rather compact and occupies the entire space between the epidermal layers not taken by the bundles. Stomata are found on both surfaces of the leaf.

SPARTINA CYNOSUROIDES. — Upper surface of the leaf much furrowed. Epidermis composed of small cells with rather thick walls curiously thickened or elongated on the outside, forming papillae or short hairs mostly with truncate or blunt points. At the bottom of each furrow are three rows of large colorless cells for storing water.* The stomata are situated on either side of this row of cells near the bottom of the furrow. Lower epidermis consists of small cells with very thick walls on the outside, nearly smooth. Subepidermal strands of stereome-cells occur above and below each mestome bundle, and each of the larger bundles is provided with a stereome sheath inside the sheath of green parenchyma which encloses all mestome bundles. The stereome sheath is entirely wanting in some of the small mestome bundles and is partially developed in others. There is no distinct keel, but the median mestome bundle is slightly larger than the others and has larger strands of stereome above and below it. The stereome sheath is also well developed, but the cells of the parenchyma sheath are rather small. A layer of thick-walled cells separates the leptome and hadrome.

CYPERUS FILICULMIS. — Leaf is conduplicate on drying. Very large colorless water-cells occur on superior surface: those in the center directly over the midrib are largest and all have rather thick outer walls with very thin partition walls between the cells. The sections studied had eleven mestome bundles, five on either side of the midrib. A subepidermal strand of stereome occurs

* O'Brien, *l. c.*

on the under surface opposite nearly every mestome bundle, and on the upper surface each side of the bulliform cells. Bundle of the keel is partly surrounded by a sheath of stereome. Each mestome bundle has a sheath of large green parenchyma-cells. Epidermis of edges and under surface composed of small cells with rather thick outer walls. Stomata all on under surface, not depressed. Chlorenchyma-cells are arranged radially around the mestome bundles. On each side of the bundles and alternating with them is a row of cells or ducts containing a brown substance, probably tannin. A transverse section of the leaf is figured (*pl. 26, d*).*

STENOPHYLLUS CAPILLARIS. — Leaf has six rows of bulliform cells on the upper surface above the keel. There are only three bundles, one in center, and one on each side. There are five stereome strands, two on upper surface at edges of the layer of bulliform cells, and three on lower surface, one in keel and one on each side opposite those of the upper surface. Epidermis of lower and lateral surfaces is made up of small cells with rather thick walls. Each bundle has a sheath of stereome inside of which is a sheath of green parenchyma-cells. The central vascular bundle has the elements well developed but in the other mestome bundles the leptome and hadrome are not well differentiated. Stomata occur in the hollows of the lower surface each side of the keel and along the lateral surfaces between the stereome strands. Occasionally an upper or lateral epidermal cell is prolonged into a short, stout spine or hair. Certain cells or vessels are filled with a brown substance, probably tannin, similar to that found in *Cyperus filiculmis*. The assimilating cells radiate from the vascular bundles. A cross-section of the leaf is shown (*pl. 26, f*).

The stem is star-shaped in transverse section, having five points, a heavy strand of stereome occurring beneath the epidermis of each point, and opposite a vascular bundle. Two of the bundles are larger than the other three and have the elements well developed; the three smaller ones are not clearly divided into leptome and hadrome. Each bundle has a stereome sheath with sheath of green parenchyma inside like the leaf-bundles. Epidermis is made up of colorless cells with rather thick outer walls. These cells

* See also O'Brien, *l. c.*

are small over the ridges but large in the grooves and probably function as bulliform cells. Stomata occur in the center of each groove. Central portion between the vascular bundles is composed of large pith-cells. Certain cells or vessels, as in the leaf, contain a reddish or brown substance. These are called tannin cells by Holm, who has figured the stem in transverse section and described in detail the structure of the whole plant of this as well as of other North American species included by him in the same genus (*Fimbristylis*).*

CAREX PENNSYLVANICA. — Leaf is conduplicate on drying. Epidermis consists of small colorless cells larger on upper than on lower surface, and much enlarged over the keel, probably having the function of bulliform cells; outer walls are thick while the partition walls between the cells are thin. There are eleven mestome bundles, five on each side of the median one, which is slightly larger than the other mestome bundles, and is provided with a sheath of small parenchyma-cells replaced on the upper side by sclerenchyma-cells and on the lower by a large strand of stereome which forms the keel. The mestome bundles have sheaths of small parenchyma-cells and six of them are reinforced by strands of stereome both above and below. Between each pair of bundles (five on each side of keel) is a strand of large colorless thin-walled cells (parenchymatous tissue) which is probably for the storage of water.† Stomata occur on lower surface.

CAREX MUHLENBERGII. — Epidermal layer of upper surface is composed of rather large colorless cells, uniform in size except where partially interrupted over some of the stereome strands opposite the mestome bundles. The cells of the lower epidermis are much smaller. The bundles are small and the material studied had one bundle in the keel and nine on each side, making nineteen in all. Subepidermal strands of stereome occur on the keel, and above and below some but not all of the mestome bundles. Each bundle is enclosed in a green parenchyma sheath inside of which is a stereome sheath with cell lumina nearly closed. Between the mestome bundles are very large strands of water-

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* Holm, T. Am. Jour. Sci. IV. 7: 435–450, *f. 1–14.* 1899.

† Beal, W. J. The bulliform or hygroscopic cells of grasses and sedges compared. Bot. Gaz. 11: 321–326, *f. 10. pl. 10.* 1886.

holding tissue. The cell-walls are very delicate and broken down in some cases though intact in others. Holm in writing about the structure of *Carex Fraseri* * considers these strands as lacunes. Though the cell-walls may eventually break down completely, thus forming true lacunes, in the material which the writer has examined it seems that these strands must be considered as water-tissue. The water-strands are surrounded by assimilating cells. Stomata occur on the lower surface. *Pl. 26, b,* shows a transverse section of the leaf.

POLYGONELLA ARTICULATA. — Leaf nearly terete, slightly flattened. Large bundle in center surrounded by large parenchyma-cells, and about ten small mestome bundles in the outer portion of the parenchymatous tissue, which is evidently formed from the assimilating cells as the derivation was shown in the sections studied. Epidermal layer made up of large bulliform cells, certain cells being depressed and glandular (see *pl. 26, a*). Stomata are abundant around margin of cross-section. Between the epidermal layer and the central parenchyma-cells are three to four layers of assimilating palisade-cells containing chromatophores. The bundles contain spiral vessels. Central parenchymatous tissue has small intercellular spaces, and certain cells next to the palisade layer are filled with large crystals.

The stem is of similar structure, having an epidermal layer of cells for holding water, but a large number of the cells are glandular. Just inside the epidermal layer are two layers of green assimilating cells, inside of which is a more or less distinct layer of large circular cells. Next are ten bundles arranged radially in a circle. Inside the ring of bundles are large pith-cells. No stomata could be found on the stem. The leaf-sheaths or ocreae have large water-cells on the outside. Ten or eleven strands of stereome occur in the constricted places.

PLATANUS OCCIDENTALIS. — Upper epidermis of leaf is composed of rather small cells that appear rectangular in cross-section. These cells are not colorless and, as regards contents, resemble the palisade-cells. Palisade and mesophyl tissue very compact. Stomata occur on the under surface of the leaf, and both surfaces are covered especially when the leaf is young, with long branched

* Holm, T. Am. Jour Sci. IV. 3: 121–128, *pl. 4*. 1897.

multicellular hairs. These hairs have been figured by Solereder * and are very similar to the hairs of *Verbascum Thapsus*. The leaf contains no colorless water-cells.

ARONIA ARBUTIFOLIA. — The upper epidermal layer consists of large water-holding cells with even outer walls and a thick cuticle. These cells are not uniform on their inner walls but some project much farther than others into the palisade tissue. The lower epidermis is made up of small, green cells. Each bundle is enveloped in a parenchyma sheath, and stereome tissue occurs below the bundles. Radiating crystals occur in a few of the cells of the mesophyl and palisade tissues. The stomata are very small and occur on the under surface, where they are protected by long curved unicellular hairs.

SAROTHRA GENTIANOIDES. — Stem has water-holding tissue surrounding the bundle and extending outward to the epidermis in four strands. The stem has large pith-cells in the center, surrounded by the xylem, which consists of vessels and lignified cells. Outside of the xylem there is a thin layer of phloem, beyond which there is a peculiar tissue of large irregular cells with rather thick walls curiously pitted. This is the water-tissue, extending in four strands from the central portion to the epidermis. Between these strands are found the palisade-cells. Opposite the palisade-cells occur the stomata which are small and not especially protected. The water-holding cells have thickened walls, probably for the purpose of strengthening the tissues.

The leaves are opposite and are reduced to mere scales or bracts. A uniform epidermal layer covers both surfaces, and the assimilating cells occupy the space between with the small bundles running through the green tissue. The stomata and epidermal cells are much like those of the stem. Large reservoirs are found in the green parenchymatous tissue of both leaf and stem. These are the pellucid dots common to the Hypericaceae, and are supposed to contain oil.

HELIANTHEMUM MAJUS. — Epidermis of the upper surface is composed of medium-sized colorless cells; lower surface has smaller cells, most of which contain green coloring matter. Stomata are abundant on the lower surface, which is densely covered

* Solereder, H. Systematische Anatomie der Dicotyledonen, 877, *f. 184*. 1899.

with curious branched hairs. These hairs also occur on the upper surface, though not as abundantly. These hairs are nearly stellate, or radiating, but are not very closely appressed and must be of great value in preventing the loss of water. Between the branched hairs on both surfaces are small glandular hairs. The branched hairs (see *pl. 26, h*) are very similar to those of *Cistus Creticus* L. and the glandular hairs resemble those of *Cistus ladaniferus* L., both of which are figured by Solereder.* The palisade layer makes up half the thickness of the leaf and the mesophyl tissue is rather compact. Each bundle contains spiral vessels and has a sheath of parenchyma-cells.

VERBASCUM THAPSUS. — Both upper and under surfaces of the leaf are covered with peculiar branched multicellular hairs, which must be an important factor in preventing loss of moisture through transpiration. Glandular hairs which are also multicellular occur on both surfaces. The branched hairs are long, having a central axis the length of which is from twice to three times as great as the thickness of the leaf. The central axis is pointed at the apex and bears one, two or three whorls of pointed, horizontal, lateral branches.

LINARIA CANADENSIS. — Leaf narrow with revolute margins. The upper epidermis is composed of colorless cells which are extremely irregular in size and shape. Irregular papillae or wart-like projections on the surface of the leaf result from the irregularity of the cells. The lower epidermis is quite similar to the upper epidermis except under the midrib, where the cells are much larger and more regular in shape. The entire epidermal tissue is adapted for holding water. Stomata occur on both surfaces of the leaf, and are not depressed, but sometimes occur on the raised portion.

CHRYSOPSIS FALCATA. — Leaf conduplicate on drying. Epidermal cells of both surfaces nearly uniform in size and shape and with outer walls very strongly thickened. There are two palisade layers — one beneath the epidermis on each surface. Between the two palisade layers is a row of small mestome bundles surrounded by parenchymatous tissue, made up of large thin-walled mostly colorless cells. Some of these cells form sheaths for the bundles, and others occupy the space between the sheaths. Green color-

* Solereder, H. Systematische Anatomie der Dicotyledonen, 92, *f. 21.* 1898.

ing matter is found in a few of these cells, but apparently they have been developed for water-storage purposes. A large amount of this tissue surrounds the midrib. The bundle of the midrib is nearly surrounded by two strands of stereome — the larger occurring on the leptome side and the smaller on the hadrome side. Similar though smaller strands of stereome are found in connection with four of the larger mestome bundles, two of these having stereome on the leptome side only, while the other two have it on both sides of the bundle. Small glandular hairs project from the cuticle on both surfaces. External surface of the cuticle is roughened by small projections. Stomata occur on both surfaces and are slightly raised rather than depressed.

IONACTIS LINARIIFOLIUS. — Leaf is thick and rough. The entire epidermal layer of both surfaces is composed of colorless water-holding cells of uniform size much thickened on the outer walls. The thickened cuticle bears short, stout, pointed projections having openings into the cells. The two epidermal layers form about one third of the thickness of the leaf. A strand of stereome occurs on the leptome side of the bundle of the midrib. This is the only bundle in which the elements are clearly differentiated, though there are eight small mestome bundles in the leaf, four on each side of the midrib. On the keel there are three layers of nearly colorless, thick-walled parenchyma-cells. The palisade layer and mesophyl are very compact. Stomata occur on both surfaces, and have a peculiar structure with the cuticle projecting over the depressed guard-cells. The projection is slightly raised, and appears as a round hole in the leaf when examined from the surface (see *pl. 26, c*).

ANATOMY OF SUBTERRANEAN PARTS

In the following description of roots the measurements are given only for the specimens examined. It should not be inferred that the roots are uniform in size or that they have the same number of vessels. These measurements are given to show as clearly as possible the relation between the size of the root, its central cylinder and its largest vessels.

PANICUM DEPAUPERATUM.— The material examined has eight large vessels in the root with nineteen phloem patches arranged

radially outside of the vessels. Between and around the vessels and phloem patches, and in the center of the root, the tissue is made up of rather thick-walled parenchyma-cells with small intercellular spaces. Endodermis is composed of rather thin-walled cells of medium size. Cortex is made up of thin-walled cells mostly tearing off in cutting.

Diameter of central cylinder,	.29 mm.
" " largest vessels,	40 μ

PANICUM UNCIPHYLLUM.* — The sections examined show several large vessels in the root between and around which are rather thick-walled parenchyma-cells. Phloem patches are small and numerous, arranged in a circle around the vessels, which is the usual arrangement in grasses. The endodermis is well developed and is composed of large cells rectangular in transverse section; cell-walls are of medium thickness, and there are a few small intercellular spaces between the endodermis and the central tissue. There is no well-developed pericycle. The cortex is made up of large cells with very thin undulating walls. In one or two layers next to the endodermis the cells are rectangular in cross-section, but the other cortical cells are very irregular. Some of the cells in the central cylinder are filled with starch-granules.

Diameter of root,	.35 mm.
" " central cylinder,	.20 mm.
" " largest vessels,	27 μ

ANDROPOGON SCOPARIUS.— In the specimens examined there are thirteen vessels arranged in a circle half-way from the center to the periphery of the root and separated by rather thick-walled parenchyma-cells. Just outside the row of vessels are very small patches of phloem, hard to make out except by the thin cell-walls. Between these areas and the endodermis the cells are mostly empty, with rather thick pitted walls. A few cells contain starch-granules and some appear to be sieve-tubes. Endodermis prominent; cells rectangular in cross-section, walls thin on the outside but thickened peculiarly on the inside and showing lamellae and pits. Cortex consists of three or four layers of thin-walled cells rectangular in transverse section, mostly tearing off in cutting.

* See Rhodora, 3: 121. 1901.

Central portion of root is composed of mostly empty cells which appear circular in cross-section and have fairly thick walls with intercellular spaces at the angles. Structure is practically the same as is shown in the figure of *A. furcatus* (*pl.* 27, *d*).

ANDROPOGON FURCATUS.— The central portion of the root is made up of rather thick-walled pitted starch-cells, which are nearly circular in transverse section, *i. e.*, their lumina are circular and nearly uniform in size. The vessels are arranged in a circle having a diameter two thirds as great as that of the root-section. The roots examined contained eighteen vessels, the largest ones having a diameter of only 34 μ. Diameter of root is 1 millimeter. Just outside of the circle of vessels and sometimes alternating with them are the small patches of phloem elements. The endodermis has peculiar cells with the inner walls much thickened and pitted. Between the endodermis and the phloem region are starch-cells resembling those of the central portion except that the walls are thicker and more strongly pitted. This tissue corresponds to the sheath or pericycle but is not of the structure usually found in bundles. The larger vessels are the only portion of the xylem elements that can be made out in cross-section. The cortex is composed of four or five layers of thin-walled cells resembling cork, which are mostly empty and appear oblong in a cross-section of the root.

The rootstock is thickened at the nodes (see *pl.* 27, *e*), and these nodes are composed chiefly of rather thick-walled parenchyma-cells crammed with starch granules. These cells are nearly circular in cross-section and larger than the corresponding cells of the root. The vascular bundles penetrate this tissue at nearly equal distances and seem to extend in all directions, for bundles cut transversely, longitudinally and obliquely occur in the same section. These have been deflected at the thickened nodes and are parallel between the nodes. The starch-cells are usually larger than the vessels of the bundles. The latter are made up of long pitted cells. The cortex is thin and is made up of parenchyma with cells much smaller than those of the central portion and packed less closely with starch-granules. The endodermis surrounds the entire central portion of starch parenchyma-cells and bundles and its cell-walls are thickened on the inner side.

SPOROBOLUS VAGINAEFLORUS. — Small root has two large vessels and several much smaller ones. Endodermis prominent, of cells with inner walls strongly thickened showing lamellae and pits. Pericycle of thick-walled cells. Cortex made up of one or two layers of rather irregular large cells with walls of medium thickness and brown color.

Small root.	Diameter of central cylinder,	.1 mm.
	" " largest vessel,	20 μ

In larger roots there are four large vessels and two or three small ones. Some roots have three large vessels. Endodermis has cells with inner walls much less thickened than in small root, though lamellae and pits are still prominent. Cortex composed of about five layers of cells, the outer layers having thicker walls than the inner layers. No starch. Cross-sections of both large and small roots are figured on *pl. 27*, *b* and *c*.

Large root.	Diameter of entire root,	.25 mm.
	" " central cylinder,	.18 mm.
	" " largest vessels,	37 μ

POA COMPRESSA. — Young root has a single vessel in the center with rather thick-walled cells between this and the endodermis. The endodermis is composed of thick-walled lamellated cells. Outside and next to the endodermis is a layer of cells quite different from the endodermal cells and those of the cortex. These cells are oblong in transverse section, have thicker walls than the cortical cells, and of the same color as the endodermal cells. Cells of the cortex have thin walls, and are irregular in shape.

Diameter of root,	.25 mm.
" " central cylinder,	.1 mm.
" " " vessel,	17 μ

Rhizome: central portion is made up of large empty pith-cells with large intercellular spaces. This tissue is surrounded by a layer of sclerenchymatous tissue several cells in thickness with which all of the bundles are connected; some of the bundles are entirely surrounded by it, but most of them and especially the larger bundles are just inside this ring of sclerenchyma. Outside are small empty parenchyma-cells with thin walls and

small intercellular spaces, the epidermal layer having thicker walls. The sclerenchyma-cells show lamellae and pits.

SPARTINA CYNOSUROIDES. — Central portion of root is provided with vessels arranged in the form of a circle as seen in cross-section, with the phloem tissue immediately surrounding the circle of vessels. Endodermis apparent, formed of small, rather thin-walled cells joined on the outside by three or four rows of thick-walled circular cells with large intercellular spaces. From this tissue narrow strands of cells extend to the cortex, forming immense lacunes. Small simple root-hairs extend from the outer cells of the cortical layer. The central portion inside the circle of vessels is made up of rather thin-walled cells appearing circular in cross-section, with intercellular spaces at the angles. There is no starch. The structure of the root is shown on *pl. 27, f.*

Diameter of root,	1.5 mm.
" " central cylinder,	0.6 mm.
" " largest vessels,	37 μ

CYPERUS FILICULMIS. — The material examined shows a single large vessel in the center of the root surrounded by rather small cells apparently empty. Endodermis composed of very thick-walled cells next to cortex. These are light-brown in color and show both lamellae and pits. Cortex dark-brown in color and made up of large rectangular cells with rather thick walls (see *pl. 27, a*).

Diameter of root,	.15 mm.
" " central cylinder,	.11 mm.
" " vessel,	33 μ

Corm: transverse sections show it to be made up of rather thin-walled parenchyma-cells densely packed with starch. These cells are circular, hexagonal or pentagonal in shape with pitted walls. Small intercellular spaces occur at the point of union of three cells. Spiral vessels occur in the bundles, which are small and irregularly distributed throughout the central portion of the rhizome. Certain cells are filled with peculiar brown substance presumably the same as is found in the leaves. This does not dissolve upon long standing in xylol.

STENOPHYLLUS CAPILLARIS.— The material examined shows a single large vessel in the center of root, surrounded by thick-

walled cell tissue containing the phloem patches. Endodermis formed of large thick-walled cells, reddish brown in color and strongly pitted and lamellated. Cortex composed of large irregular thin-walled cells. All cells of the root are colorless.

Diameter of root,	.25 mm.
" " central cylinder,	.11 mm.
" " central vessel,	33 μ

CAREX PENNSYLVANICA.— A section of the root shows six large vessels in central portion and just outside of the region occupied by the vessels occur the phloem patches. Endodermis composed of deep narrow cells with inner walls very much thickened, with pits and lamellae. Cells of endodermis and of central portion contain starch. Outside of endodermis are several layers of thick-walled, apparently empty, brown sclerenchyma-cells, only those of the first layer having a regular form. Some of these layers are separated or pulled off in places, forming large lacunes. Outside of this tissue are three layers of thin-walled parenchyma-cells. In some cases the tissue around the lacunes has separated, and the entire gap has been filled in by parenchymatous tissue.

Diameter of root,	.65 mm.
" " central portion,	.35 mm.
" " largest vessels,	33 μ

Rhizome: central portion is composed of circular cells with rather thin pitted walls and devoid of large vessels. The bundles are arranged in a circle and the vessels are no larger than the cells in the central portion. Endodermis apparent but not distinct as in the root: cells resemble others except that they have thicker walls and have a more regular arrangement. Cortex is made up of parenchyma-cells and separates from the central cylinder. There are three distinct vascular bundles in the cortex, probably belonging to leaf-scales or to branches. Some of the cells of the central portion contain starch.

Diameter of rhizome,	.95 mm.
" " central portion,	.71 mm.
" " vessels.	20 μ

SALOMONIA BIFLORA (*Polygonatum biflorum*). — Root: bundle contains from six to eight good-sized vessels with xylem arranged

radially, the transverse section showing six points. Endodermis distinct, of rather thick-walled cells except those cells opposite the xylem rays which have thin walls, probably for the purpose of transferring water between the bundle and the parenchymatous tissue. Central cylinder is surrounded by a large mass of parenchyma-cells having thin walls and containing no starch.

Diameter of root,	.78 mm.
" " central cylinder,	.18 mm.
" " largest vessels,	40 μ

Rhizome: consists of large thin-walled parenchyma-cells in which tissue the concentric bundles are rather irregularly arranged. Vessels of the bundles are much smaller than the parenchyma-cells surrounding the bundles. A few cells contain large bundles of raphides or acicular crystals. Cells of outer portion somewhat smaller than those in central part and contain smaller crystals. Endodermis not apparent. The structure of a small root is shown on *pl. 28, a.*

VAGNERA RACEMOSA. — Root: bundle arranged radially with nine points, nine phloem patches and six large vessels. Endodermis distinct, of cells rectangular in cross-section, and with thicker walls than the cells of the surrounding tissue. Opposite the xylem points, the thick-walled endodermal cells are replaced by thin-walled cells, thus making a connection between the xylem and the cortex. The cortex is composed of very large thin-walled parenchyma-cells with intercellular spaces.

Diameter of root,	1.25 mm.
" " central cylinder,	.39 mm.
" " largest vessels,	66 μ

Rhizome : central tissue is made up of large thin-walled cells with many intercellular spaces. The bundles extend through this tissue at quite regular distances apart and are of the type found in Liliaceae and other monocotyledons with phloem enclosed in a xylem sheath of thick-walled pitted vessels. Endodermis composed of small cells. Certain large cells in the central portion contain bundles of raphides. Cortex is composed of large circular parenchyma-cells. Whole structure of roots and rhizome much like that of *Salomonia biflora*, to which it is closely allied.

CYPRIPEDIUM ACAULE. — Root has radially arranged bundle with eight xylem points, and no very large vessels. Endodermis present, of thick-walled cells which are interrupted opposite the radiating points of xylem, and replaced by thin-walled cells. The cortex is made up of very large, circular, parenchyma-cells with thin walls, and intercellular spaces. Some of the cells contain small quantities of starch. The two outside layers contain smaller cells which are rectangular in cross-section.

Diameter of root, about	2.00 mm.
" " central cylinder,	.45 mm.
" " cells of cortex,	.13 mm.
" " largest vessels,	30 μ

POLYGONUM CONVOLVULUS. — Primary structure not found in the material examined, but the secondarily thickened root is remarkable for the size of the vessels, some of which are from one sixth to one seventh the diameter of the root. There are no large parenchyma-cells in the cortex, but several strands of thick-walled cells run through the cortex near the periphery. The transverse section of a secondarily thickened root is shown on *pl. 28, c*. Roots examined were somewhat flattened.

Diameter of root,	.83 x 1.0 mm.
" " largest vessels,	106 x 166 μ

FRAGARIA VIRGINIANA. — Central cylinder is rather small and xylem elements appear triangular in cross-section, and surrounded by the phloem. Endodermis is distinct, being made up of small cells, with walls of medium thickness, filled with starch-granules. Central cylinder is surrounded by much parenchymatous tissue of large thin-walled cells mostly circular in cross-section. Cortex separates in cutting, and is made up of circular cells a trifle smaller than the parenchyma-cells and with thicker walls. Certain cells of the cortex, parenchyma and central portion contain brown granules; such cells are also found between the xylem vessels, and several cells near the endodermis contain a brown or yellow substance resembling resin. Abundance of parenchymatous tissue must be of considerable use in storing water.

Diameter of root,	1.00 mm.
" " central cylinder,	.25 mm.
" " largest vessels,	27 μ

POTENTILLA CANADENSIS. — Primary structure shows three vessels in the bundle surrounded by thin-walled cells — the phloem. Endodermis is composed of large cells nearly circular in cross-section, with dark walls of medium thickness. Pericycle of smaller cells with light-colored walls. The bundle begins as a diarch. The cortical cells are very large and irregular in shape with thin undulating walls. Older root shows three-pointed xylem with alternating phloem patches. No endodermis immediately surrounds the bundle, but near the periphery of the section is a layer of small rectangular cells greatly resembling an endodermis. These cells are closely packed with starch. Between this layer and the xylem of the bundle the tissue consists of rather thick-walled parenchyma-cells, most of which appear empty, but a few are densely packed with granules.

Diameter of root,	.18 mm.
" " central cylinder,	.1 mm.
" " largest vessels,	13 μ.

CROTALARIA SAGITTALIS. — Primary structure not observed. Roots in which secondary thickening has taken place have from twenty-five to thirty large vessels arranged irregularly. Strands of thick-walled sclerenchyma-cells run through the cortex near the periphery and some similar cells occur in the central cylinder. Resembles *Cassia* very closely in structure, but the sclerenchymatous tissue is more abundant than in *Cassia*. Shown on *pl. 28, d.*

Diameter of root (thickened),	.1 mm.
" " central cylinder,	.5 mm.
" " largest vessels,	46 μ.

LUPINUS PERENNIS. — Central cylinder of the root is oval in cross-section, and small for the size of the root. Xylem has the diarch arrangement whith phloem on both sides. Sclerenchyma strands appear in connection with the phloem tissue. Endodermis is apparent, though the cells are rather irregular and have thin walls. Outside the endodermis the root is made up of very large thin-walled parenchyma-cells, the largest cells having a diameter of 50 μ. Cortex consists of a single layer of small thin-walled cells with small brown granules.

Diameter of root,	.5 mm.
" " central cylinder (oval),	.2 x .3 mm.
" " largest vessels,	20 μ.

MEIBOMIA sp.—The primary root shows three large vessels and three smaller ones in the bundle which seem to be entirely surrounded by phloem. The phloem contains several strands of sclerenchyma-cells with closed lumina. The endodermis is composed of oblong thin-walled cells. The pericycle consists of similar but smaller cells. The cortex has very large cells with thin undulating walls and some intercellular spaces. Considerable lignified tissue is formed in the secondarily thickened roots and the vessels are large.

Diameter of root,	.31 mm.
" " central cylinder,	.18 mm.
" " largest vessels,	30 μ.

CASSIA CHAMAECRISTA.—Most of the preserved material shows secondary thickening in the roots, but the root from a young seedling exhibits the primary structure. In the latter there are four large vessels, one in the center and the others around it forming a three-pointed xylem in transverse section. This is surrounded by the phloem. Endodermis is prominent, of good-sized cells, oblong to circular in cross-section, and with walls only slightly thickened. Just inside the endodermis and near the three radiating xylem points are three strands of sclerenchyma-cells. The lumina are nearly closed and the lamellae can be distinguished. The cortex is composed of large parenchyma-cells with thin undulating walls.

Diameter of entire seedling root,	.3 mm.
" " central cylinder,	.16 mm.
" " largest vessels,	66 μ.

In roots which have undergone secondary thickening, the vessels are large and numerous, varying from thirty-six to fifty in the sections examined and probably even more in larger roots. These vessels are pitted, approaching scalariform. About half of the small xylem-cells in the center between the vessels stain dark after standing for a long time in chloriodide of zinc, though these were not stained at first by this reagent. They are probably parenchyma xylem-cells with cellulose walls which stain only after standing

for a long time. There are curious strands of lamellated sclerenchyma-cells with narrow lumina running through the cortex near the periphery. None of the cells contain starch.

Diameter of entire root,	.9 mm.
" " largest vessel,	66 μ.

VIOLA SAGITTATA. — The xylem is surrounded by phloem, though very young roots show the diarch arrangement. Endodermis present, composed of small rather irregular thin-walled cells. Cortex is made up of larger cells which have thicker walls. A few of the cortical cells are filled with a dark-brown substance.

Diameter of root,	.6 mm.
" " central cylinder,	.25 mm.
" " largest vessels,	23 μ.

ONAGRA BIENNIS. — Real primary structure not found, but sections of small roots show a number of large vessels in central portion surrounded by woody tissue. Around this is the phloem containing many large cells or vessels with raphides. On the outside of the phloem tissue are two distinct layers of phellogen, the cells being large, nearly uniform in size, and rectangular in cross-section. These cork-cells have thin dark-colored walls and have developed from the pericycle, according to Strasburger (Lehrbuch der Botanik, ed. 5, 119), and have crowded and flattened the endodermal cells beyond recognition. These flattened endodermal cells may be found on the outside of the cork layer. In one section the cork-cells have not yet fully developed and the endodermal cells still remain. Several layers of cork-cells occur in older roots. Outside of the cork layer are several layers of much flattened cells which peel off in handling and are probably the bark. The cells have brown walls.

LYSIMACHIA QUADRIFOLIA. — Several small vessels but no very large ones are found in the center of the root. The phloem patches are five in number and close to the endodermis. Endodermis is composed of cells that appear oval or oblong in cross-section; the walls are quite thick and are lamellated and pitted. The pericycle is made up of similar though slightly smaller cells. In the center of the root there is a group of sclerenchyma-cells with very thick walls which are lamellated and pitted. The corti-

cal cells are rather large, with thin undulating walls and very small intercellular spaces. The outer layer has cells of much more regular shape than the others, and some are prolonged into unicellular root-hairs. Throughout the whole root but especially numerous in the center are certain cells filled with a dark-brown substance, resembling tannin, but which is probably a resin, as Bary refers to resinous substances in the roots of other members of the genus.* Roots which have undergone secondary thickening show a large group of thick-walled, probably lignified cells in the center, outside of which is a zone containing the xylem and phloem patches. Running through this zone are radial strands of lignified cells and one or two rows next to the cortex. The cortex is made up of cells which are oval or oblong in cross-section with intercellular spaces. With the exception of the outer layer which has colorless cells, the cell-walls are brown in color though none of the cells as in the primary root are filled with tannin.

Diameter of root,	.65 mm.
" " central cylinder,	.25 mm.
" " largest vessels,	23 μ.

Rhizome: The central portion is made up of pith-cells nearly circular in cross-section. Some of these are colorless but many are filled with small brown granules, while others are entirely filled with the brown substance. A thin layer of small-celled sclerenchymatous tissue surrounds the pith. The cortex is formed of large circular cells, much resembling the pith-cells, and many contain resin. Large intercellular spaces occur in the cortex. Half way from the sclerenchymatous layer to the periphery is a row of ducts or intercellular passages containing resin. The outside of the rhizome is covered with what appear to be simple hairs.

ASCLEPIAS VERTICILLATA. — The bundle of the root contains no large vessels, but there are many small ones. Endodermis can be made out in specimens studied, though it is evident that secondary thickening of the root has commenced. The cells are oblong in transverse section and have thin walls. The xylem has

* Bary, A. de. Vergleichende Anatomie der Vegetationsorgane der Phanerogamen und Farne, 219. 1877.

four points in young root. The cortex is made up of large cells circular in cross-section and with many intercellular spaces towards the periphery; near the central cylinder the cells are oblong and the tissue much denser. Most of the cells are closely packed with starch.

Diameter of root,	1.2 mm.
" " central cylinder,	.32 mm.
" " largest vessels,	27 μ.

TRICHOSTEMA DICHOTOMUM. — Very small root shows that the bundle began as a diarch, with endodermis composed of thin-walled cells rectangular in transverse section. The cortex cells are thin-walled, colorless and very large. Roots that have undergone secondary thickening have many large vessels with pitted walls. In the sections studied there were from forty-five to fifty of these vessels that were distinctly larger than the other xylem cells. Structure of root shown on *pl. 28, b.*

Diameter of root,	.9 mm.
" " central cylinder,	.65 mm.
" " largest vessels,	60 μ.

VERBASCUM THAPSUS. — Small root has a number of small vessels in the center surrounded by phloem. Endodermis prominent, cells oblong in transverse section. Cortex is made up of very large thin-walled cells. Older root has a large central cylinder, containing many pitted vessels of rather small size. The endodermis can still be made out in some sections. The cortex now consists of several layers of small cells which are oblong in cross-section, and nearly free from starch.

Diameter of root,	.13 mm.
" " central cylinder,	.5 mm.
" " largest vessel,	5 μ.

LINAȒIA LINARIA. — Small root shows phloem surrounding the xylem. Endodermis present. Cortical cells are very large and mostly colorless, but a few are filled with brown granules. Secondarily thickened roots have several large vessels with measurements as follows:

Diameter of root,	.72 mm.
" " central cylinder,	.5 mm.
" " largest vessels,	36 μ.

LINARIA CANADENSIS. — Primary root shows three vessels in center surrounded by phloem. Endodermis distinct, of small cells that appear oblong in cross-section. Outside of the endodermis are three rows of very large cortical cells, circular, pentagonal or oblong in transverse section. In secondarily thickened root the vessels are not large, and are pitted. The cortex is a thin layer of large thin-walled cells.

Diameter of root,	.09 mm.
" " central cylinder,	.02 mm.
" " largest vessels,	4 μ.

CHRYSOPSIS FALCATA. — A cross-section of the xylem of the primary root shows a four-pointed radial arrangement, with two large vessels and two small ones in the center. Endodermis apparent, cells nearly circular in transverse section, with thin walls. Pericycle of similar structure. The cortical tissue is formed of about eleven layers of large colorless parenchyma-cells, circular in cross-section, with thin walls, and intercellular spaces. Walls of the two outer layers are brown in color.

Diameter of root,	.45 mm.
" " central cylinder,	.13 mm.
" " largest vessels,	17 μ

SOLIDAGO NEMORALIS.— Bundle has diarch arrangement in young root, and the vessels are very small. Endodermis is apparent, and the cortex is made up of large cylindrical cells with contents plainly visible. In roots that have undergone some secondary thickening there are several good-sized vessels and the cortical cells are large and colorless with large intercellular spaces, while the endodermis can still be made out. The structure closely resembles that of *Chrysanthemum Leucanthemum.*

Diameter of root,	.55 mm.
" " central cylinder,	.26 mm.
" " largest vessels,	43 μ

IONACTIS LINARIIFOLIUS. — Primary structure of root has a bundle with three-pointed xylem in cross-section and containing three large vessels. Endodermis is prominent and is composed of thin-walled cells which vary from rectangular to circular in

cross-section. The cortical tissue is made up of large, circular, colorless cells with rather thick walls and large intercellular spaces.

Diameter of root,	.46 mm.
" " central cylinder,	.15 mm.
" " largest vessels,	20 μ

LEPTILON CANADENSE. — Central cylinder contains three vessels in primary root. The endodermis is prominent, being made up of thin-walled cells that are rectangular in cross-section. The pericycle is formed of similar but smaller cells. The cortical tissue is very similar to the structure found in other composite roots, and consists of large thin-walled circular cells with large intercellular spaces. The outside layer has thicker walls.

Diameter of root,	.2 mm.
" " central cylinder,	.1 mm.
" " largest vessels,	13 μ

ANTENNARIA NEGLECTA. — Transverse section of the xylem is a radial five-pointed star with phloem patches between the points. There are no large vessels. The endodermis is apparent, with cells nearly circular in cross-section and walls only slightly thickened. The pericycle is composed of similar but smaller cells The cortical tissue is made up of from fourteen to fifteen layers of rather large colorless cells oblong in transverse section.

Diameter of root,	.85 mm.
" " central cylinder,	.25 mm.
" " largest vessels,	17 μ

CHRYSANTHEMUM LEUCANTHEMUM.— Bundle has radial arrangement, with four xylem points and four phloem patches. The vessels are not large. Endodermis composed of thin-walled cells. The cortex is formed of very large colorless thin-walled parenchyma-cells with large intercellular spaces. The peripheral layer is of a brown color.

Diameter of root,	.56 mm.
" " central portion,	.23 mm.
" " largest vessels,	17 μ
" " cortical cells,	33 μ

ARTEMISIA CAUDATA. — One very large vessel in the center is surrounded by several smaller vessels and lignified cells show-

ing lamellae. The phloem surrounds this tissue. Endodermis is still present, though secondary thickening has evidently begun, in the roots examined. Cells of the cortex are hexagonal and pentagonal in shape, are very large and have thin walls. The structure of the root is quite similar to the root-structure of the other members of the Compositae that have been examined in preparing this paper.

Diameter of root,	.51 mm.
" " central cylinder,	.28 mm.
" " largest vessel,	33 μ

THE STRUCTURE CONSIDERED IN RELATION TO THE ENVIRONMENT

It is commonly known that the different kinds of plants differ in their minute structure as well as in their external gross appearance, though in most cases to a less marked degree. Nearly all of the works on structural botany contain figures illustrating the various plant tissues and forms of cells. The functions of most of these specialized tissues have been known for many years, but the variations were regarded as properly belonging to different species of plants instead of as special adaptations for the benefit of the plant that might finally lead to the erection of species. It has been during the last few years only that we have looked upon plants as being capable of great modification by environment, even as regards external characteristics. Much more recently has it been shown that histological differences, which fundamentally precede gross external differences, are the result of environment. Under favorable conditions perhaps we do not notice the changes so much, but when the conditions become unfavorable it will always be found that certain plants have been able to live where others have perished, and all because of slight variation in some direction which proves beneficial. So natural selection acting through many generations has preserved these beneficial variations, which through the laws of heredity and by the aid of continued natural selection have reached a higher and higher development.

Thus we have in aquatic plants specially developed air-passages and bladder-like floating tissues. Hydrophytes of fresh water also differ from those of salt water (halophytes) in their cell structure.

Desert plants (xerophytes) have many peculiar adaptations for the conservation of water. Large parenchyma-cells, or increased palisade tissue, become abundant, in many cases forming a fleshy or succulent plant which reaches the highest development in the Cactaceae.

But many plants have developed special cells for water-holding purposes, while others through their root system have provided a ready means of taking up water and some have a combination of both arrangements. This is known as a xerophytic structure and is found in desert plants, though it is not uncommon to find a similar structure in beach plants or even hydrophytes. *Salicornia* and certain species of *Atriplex* which have succulent stems or leaves will serve to illustrate this point. It has been explained that, as these plants commonly grow on salt marshes and are often covered by the tide, on account of the saltness of the water the plants may not be able to make use of it and really depend upon showers and the dew for their water supply; hence the necessity of conserving this until more water may be obtained.

It is also claimed that swamp plants develop similar structures on account of the accumulating quantity of acid derived from the humus of the soil through chemical changes in it; that even swamp plants on account of this acid may not be able to obtain plenty of pure water and these structures are developed for the purpose of economy in using it.

Be this as it may, the fact remains that we do find the same or similar structures in plants of quite different habitats. Cowles found that willows, which are perhaps the most typical of swamp trees, were best able to adapt themselves to the conditions of the advancing sand dunes of Lake Michigan * because when partially buried by the sand to the depth of many feet the tree put out new roots and was not injured. Many other trees like oaks and pines were killed. Schimper goes still farther in showing the similarity between xerophytes and bog plants, and also states that there are no structural differences by which we can distinguish xerophytes from halophytes. Where differences exist they are chiefly physiological in character and relate to the effect of light, heat and a moist or dry air upon the plant. "Physiological dampness then

* Cowles, H. C. Bot. Gaz. 27: 292. 1899.

is correlated with a hydrophytic, and physiological dryness with a xerophytic vegetation." *

With this brief general survey of the subject we will now discuss the ecological structure of some of the plants of the North Haven sand plains.

A number of perennial plants, of which the milkweeds (*Asclepias*), *Lespedeza*, *Baptisia tinctoria*, *Lupinus perennis*, *Cracca Virginiana* and *Meibomia* are good examples, have long roots that go down deep into the subsoil and bring up moisture from a lower level to supply the needs of the plants. Clovers also do this and are often able to withstand drought and even make growth when other plants fail and perish. *Asclepias Syriaca* and *A. amplexicaulis* grow quite luxuriantly upon the sand and in no small measure must this be attributed to the deep growing roots and rhizomes, which are not only able to obtain water but may hold it for some time or until it can be used by the plant. (*Pl. 24, b*, shows a colony of *Asclepias Syriaca.*) *A. verticillata* is not a deep-rooted plant, but the roots are fleshy and the leaves have a narrow form exposing much less surface than the broad-leaved species. The milky juice of these plants, while not thoroughly understood, seems to be correlated with other xerophytic characters and probably prevents the escape of water. If the plant is cut or wounded the milky juice soon closes over the wound, forming an impervious rubber-like coating. On account of this substance many plants with a milky sap, like *Lactuca*, *Asclepias* and *Euphorbia*, will wilt when cut and placed in water, because the water cannot enter the stem through the coating formed by the milky juice.

Some of the legumes in addition to their habit of deep-rooting, have the surface of stem and leaves well protected by hairs. *Lespedeza Stuvei* and *Cracca Virginiana* are good examples.

A fleshy leaf has been considered the most perfect type of xerophytic adaptation, and this is found in *Polygonella articulata* and to some extent in *Euphorbia polygonifolia.*

In *Cypripedium acaule* and certain liliaceous plants like *Salomonia* (*Polygonatum*) and *Vagnera* (*Smilacina*) there is some degree of fleshy development of the leaf and stem tissues. We find also

* Schimper, A. W., *l. c.* 4.

that these last named plants have thick fleshy roots and rhizomes that can, doubtless, store water as well as food. These plants also have thin-walled cells in the endodermis of the small roots opposite the xylem rays, in order to permit the rapid transfer of water between the xylem and cortex.

Linaria Canadensis, which is abundant at North Haven around the barren tract, making the field fairly blue in June, has leaves that are linear in shape and somewhat succulent. Another class of plants, to which belong several members of the Compositae, and of which *Ambrosia artemisiaefolia*, *Artemisia caudata* and *Achillea Millefolium* may be mentioned, possess finely divided leaves which are more or less hairy as a means of reducing the loss of water.

Ionactis linariifolius and *Chrysopsis falcata* have narrow rigid leaves exposing a minimum amount of surface and seem well fitted for dry situations. A microscopical examination of the leaves exhibits special adaptations for conserving the moisture which they contain. Both have a much thickened cuticle and in the former the stomata are well protected, while the leaf of the latter has a palisade layer beneath the epidermis of each surface.

Sarothra gentianoides (*Hypericum nudicaule*) has the leaves reduced to mere scaly bracts and the stem contains special water-holding cells with thick walls peculiarly pitted and green assimilating cells that enable it to perform the function of leaves. The root system contains large vessels and is well developed for the rapid supplying of water.

The frost flower, *Helianthemum majus*, a common plant of the sand plains, has stem and leaves well protected from excessive loss of water by a dense covering of appressed radiating hairs (see *pl. 26, h*). The mullein, *Verbascum Thapsus*, has both surfaces of the leaf covered by long branching multicellular hairs, which must be a great protection from the loss of water. Similar hairs are found on the leaves of *Plantanus occidentalis*, and are figured by Solereder. * *Antennaria neglecta* and *Gnaphalium obtusifolium* (*G. polycephalum*) have a woolly covering of white hairs on the under side of the leaves where the stomata are situated.

It is in the histology of the grasses and sedges, however, that

* Solereder, H. Systematische Anatomie der Dicotyledonen, 877, *f. 184*. 1899.

we find the most interesting and most striking examples of special adaptations to xerophytic conditions. These adaptations result chiefly in the development of special water-holding cells or tissues in certain parts of the leaf or stem. In *Spartina* large colorless water-cells, called bulliform cells, are found at the bottom of the grooves of the upper surface of the leaf. The stomata are situated along the slopes of the groove and when the bulliform cells give up their water the grooves close up, thus preventing in a large measure the further escape of water through the stomata. Strands of stereome and a thickened and rugose cuticle are common in the graminaceous xerophytes.

Spartina cynosuroides though an inhabitant of meadows and marshes is capable of growing on the sand plains, as it is found at Montowese. The microscopic anatomy of the leaf shows this grass to have a typical xerophytic structure as pointed out by O'Brien.* The roots have developed large lacunes (*pl. 27, f*), which primarily were probably for purposes of aëration. It is doubtful if these lacunes can be of any use to the plant under xerophytic conditions.

Andropogon scoparius exhibits a well-marked xerophytic structure, as special water-cells occur on the upper surface of the leaf (*pl. 26, g*). The same may be said of *A. furcatus*, which has a similar though less fully developed xerophytic structure of the leaf. The root structure of this plant compensates for what the leaf tissues may lack in reservoirs for the storage of water. A portion of the root is perennial and the thickened nodes are stored with starch for the nutriment of the plant the following season. The appearance of these thickened rhizomes and the cell structure of the small roots are shown on *pl. 27*.

Cenchrus tribuloides also shows a well-developed xerophytic structure in the leaf. *Sporobolus vaginaeflorus* likewise is well fitted by the structure of both leaf and root to inhabit desert places. Many water-holding cells appear in the leaf and the root is provided with a very thick-walled endodermis, especially in the small root. Large roots show a modification of the structure in favor of thinner walls.

The sedges examined have the inside wall of the endodermal

* O'Brien, MSS. (see fifth footnote on p. 585).

cells very strongly thickened. This would seem to prevent the escape of moisture from the central cylinder to the outer portion in dry times, as the only means of transferring the moisture is through the pits. The sedges also have interesting structures of leaf and stem. *Stenophyllus capillaris* exhibits large water-cells on the upper surface of the leaf, which is almost reduced to linear. The stem is star-shaped in cross-section with stereome strands on the points and water-cells and stomata in the grooves. *Cyperus filiculmis* (*pl. 26, d*) has very large bulliform cells over the midrib, and when these cells lose their water the leaf folds. It also has a corm or tuberous root which is closely packed with starch and is doubtless a storehouse for both food and water. A very different leaf structure is found in *Carex Pennsylvanica* and *C. Muhlenbergii*, both inhabitants of the sand plains. Instead of the epidermal cells being very large for holding water there are several strands of colorless thin-walled cells running through the interior structure of the leaves between the mestome bundles. Though these strands seem to be regarded as lacunes, and in fact are called lacunes by most writers, they are not true lacunes, as they are spanned by delicate and undulating cell-walls in most of the material examined. In some cases these were broken down, but this might readily have occurred in cutting the hand sections. The writer considers these strands as internal water-storage tissue.

In his "Report on a Botanical Survey of the Dismal Swamp Region," Kearney mentions the rosette form of *Linaria Canadensis*.* Certain other biennials like *Verbascum Thapsus, Onagra biennis* and *Artemisia caudata* exhibit the rosette habit during the first year and is doubtless of some value in preventing a loss of water through transpiration. The habit of these four species was observed by the writer on the North Haven sand plains.

But it is the annual plants with shallow root-systems, and having a short period of growth, that must suffer most in a time of severe drought. Such plants have woody roots in which the primary structure disappears early and the vessels are large and numerous. Annual legumes are of this class, and the roots of *Cassia Chamaecrista, Crotalaria sagittalis* and *Strophostyles helvola* show a number of large vessels in the secondarily thickened roots.

* Kearney, T. H. Contr. U. S. Nat. Herb. 5 : 386. 1900.

Strands of sclerenchyma in the cortex are commonly found in these plants and are thought to be of value in strengthening and preserving the shape of the plant in excessive drought and wilting of the tissues. In size and number of vessels the root structure of *Trichostema dichotomum* is similar to that of the annual legumes, but the sclerenchymatous strands are wanting. *Polygonum Convolvulus*, *Ambrosia artemisiaefolia* and *Sarothra gentianoides* have even larger vessels than the plants just mentioned, and seem to have nearly reached the limit of power to supply water to the upper portion of the plant.

In the small lateral roots of perennial composite plants we find much cortical tissue of colorless cells that can doubtless store water to be used later by the plants. Moreover, the plants of this family whose roots were studied inhabit dry regions. This is true of *Chrysanthemum Leucanthemum*, *Chrysopsis falcata*, *Ionactis linariifolius*, *Artemisia caudata* (biennial), *Solidago nemoralis*, *Antennaria neglecta*, *Gnaphalium obtusifolium* (*G. polycephalum*) and *Leptilon Canadense.*

In *Salomonia biflora* and *Vagnera racemosa* the endodermis of the small roots is interrupted or has some of its cells replaced by thin-walled cells opposite the points of the xylem as they appear in cross-section. This arrangement seems to provide for the transfer of water between the xylem and the cortex.

ACKNOWLEDGMENTS

The author here expresses his gratitude to Mr. Luman Andrews, of Southington, for kindly determining the species of *Panicum* and *Sporobolus vaginaeflorus;* to Mr. M. L. Fernald, of the Gray Herbarium, for identifying *Carex Pennsylvanica;* to Mr. L. M. Tarr, local forecast official of the New Haven office of the U. S. Weather Bureau, for furnishing the records of temperature and precipitation; especially is he indebted to Professor A. W. Evans for many kind suggestions in planning and carrying out these studies, for verifying the author's determinations of plants, for help in determining several species, and for examining the microscopical preparations and the manuscript.

YALE UNIVERSITY.

a. Andropogon scoparius, North Haven.

b. Baptisia tinctoria, Montowese.

VEGETATION OF THE NORTH HAVEN SAND PLAINS.

a. Black oaks at North Haven.

b. A mound of milkweeds, *Asclepias Syriaca*, Montowese

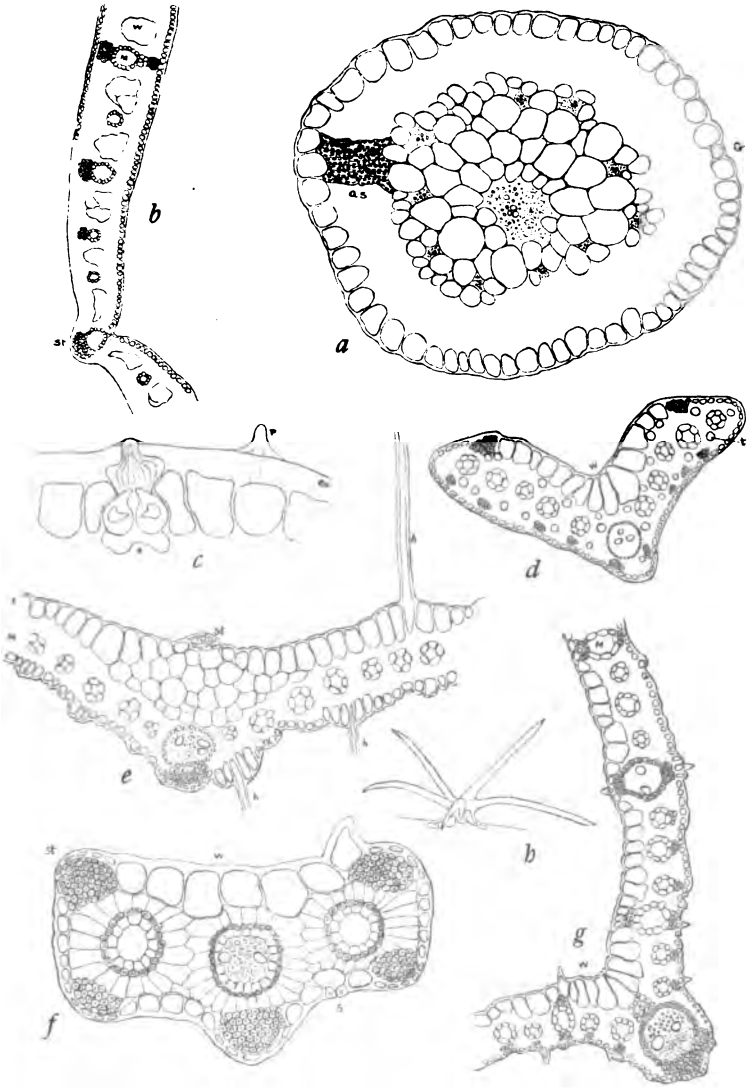
VEGETATION OF THE NORTH HAVEN SAND PLAINS.

a. A carpet of *Sarothra gentianoides*, North Haven.

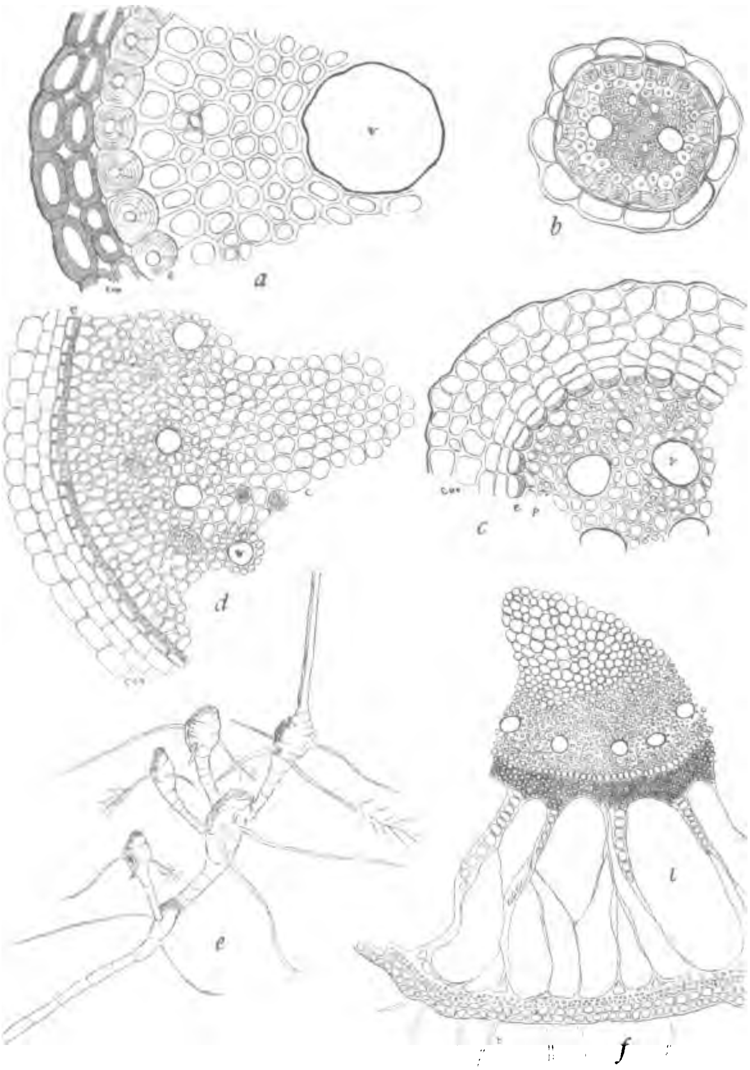
b

c

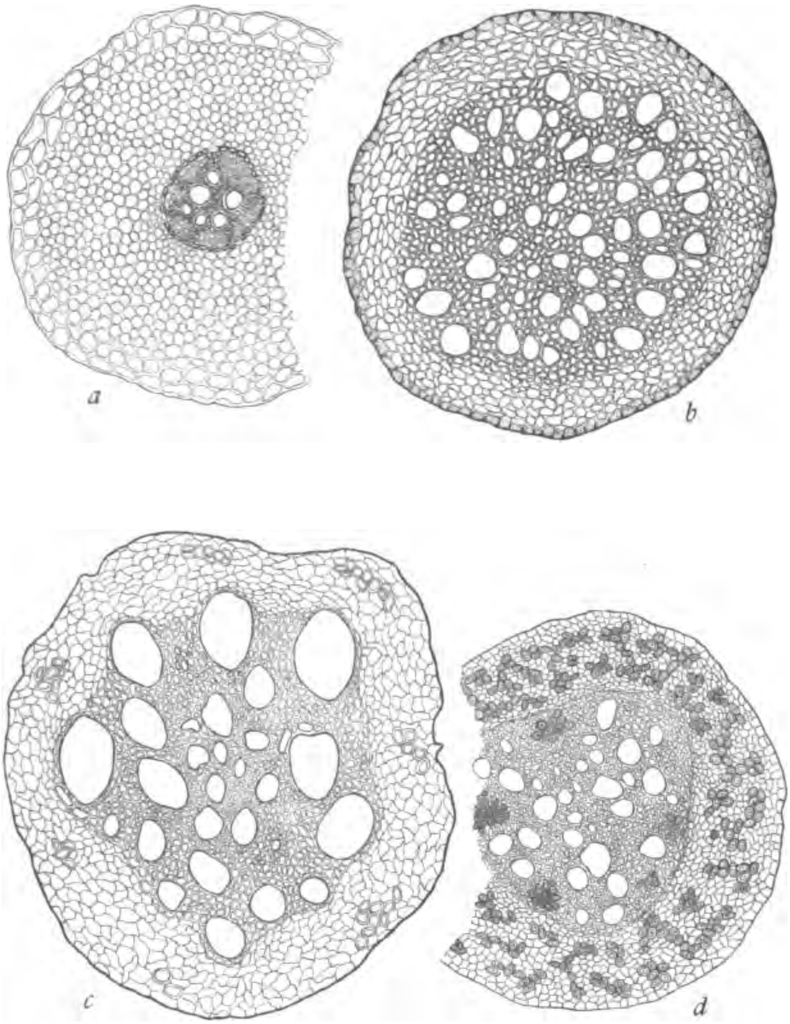
VEGETATION OF THE NORTH HAVEN SAND PLAINS.



VEGETATION OF THE NORTH HAVEN SAND PLAINS



VEGETATION OF THE NORTH HAVEN SAND PLAINS.



VEGETATION OF THE NORTH HAVEN SAND PLAINS.

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Explanation of Plates

PLATE 23

a. Tufts of *Andropogon scoparius* at North Haven. Most of the trees are black oaks (*Quercus velutina*).

b. A patch of *Baptisia tinctoria* at Montowese. Scattered about are plants of *Lespedeza capitata* and *Asclepias Syriaca*, while in the foreground the ground is covered with young seedlings of *Trichostema dichotomum* and *Sporobolus vaginaeflorus*.

PLATE 24

a. General view at North Haven, showing black oaks (*Quercus velutina*) growing in the sand.

b. A mound of milkweeds (*Asclepias Syriaca*) at Montowese. Between the plants are young seedlings of *Sporobolus vaginaeflorus*. The mound is about two feet higher than the level of the surrounding sand.

PLATE 25

a. A carpet of *Sarothra gentianoides* at North Haven. A red cedar stands in the foreground at the left and in the left middle distance may be seen a crescent-shaped mound of *Aronia arbutifolia*. In the middle distance at the right is a bunch of *Andropogon furcatus*.

b. View at Montowese showing how the sand has been blown away leaving the roots exposed. The mound is four or five feet higher than the level of the surrounding sand and the vegetation is red cedar (*Juniperus Virginiana*), black oak (*Quercus velutina*) and poison ivy (*Rhus radicans*).

c. Red cedar (*Juniperus Virginiana*) at North Haven, showing the effects of winds and storms in blowing and washing away the sand and exposing the roots.

PLATE 26

a. Transverse section of leaf of *Polygonella articulata*, showing epidermal layer of water-cells and central water-holding tissue. The assimilating cells occupy the space between the epidermal layer and the central tissue. *as*, assimilating tissue; *g*, glandular cell. $\times 70$.

b. Transverse section of the median portion of the leaf of *Carex Muhlenbergii*, showing the strands of water-tissue inside the leaf. *w*, water-tissue; *m*, mestome bundle; *st*, stereome strand. $\times 36$.

c. Portion of epidermal layer from leaf of *Ionactis linariifolius* showing peculiar thickening of the cuticle and a protected stoma. *cu*, cuticle; *s*, stoma; *p*, projection of the cuticle showing opening into cell. $\times 325$.

d. Transverse section of leaf of *Cyperus filiculmis* showing water-cells on upper surface and tannin ducts. *w*, water-cells; *t*, tannin ducts. $\times 70$.

e. Cross-section of median portion of leaf of *Syntherisma sanguinalis*. *e*, epidermal layer of water-cells supported over midrib by about three others of similar tissue; *st*, stereome; *m*, mestome bundles; *h*, hairs. $\times 70$.

f. Transverse section of leaf of *Stenophyllus capillaris*. *w*, water-cells of upper surface; *st*, stereome strands; *s*, stoma. $\times 175$.

g. Transverse section of the median portion of a leaf of *Andropogon scoparius*. *w*, water-cells of epidermal layer; *m*, mestome bundles. $\times 70$.

h. Hairs from leaf of *Helianthemum majus*. $\times 70$.

PLATE 27

a. Transverse section of a portion of the root of *Cyperus filiculmis*, showing single vessel in the center and thick-walled endodermis. *v*, vessel; *e*, endodermis; *cor*, cortex. × 550.

b. Section of small root of *Sporobolus vaginaeflorus*, showing endodermis with inner walls mnch thickened, thick-walled pericycle and very large cortical cells. × 175.

c. Transverse section of a portion of a large root of *Sporobolus vaginaeflorus*, showing four large vessels in the central portion. *v*, vessel; *p*, pericycle; *e*, endodermis with wall thickened but less so than in small root; *cor*, cortex. × 175.

d. Transverse section of the root of *Andropogon furcatus*, showing vessels, endo dermis, central and cortical tissues. *c*, central cells mostly filled with starch; *e*, endodermis with inner walls of cells thickened; *cor*, cortex; *v*, vessel. × 115.

e. Gross appearance of rootstock of *Andropogon furcatus*, showing thickened nodes. Reduced.

f. Transverse section of a portion of the root of *Spartina cynosuroides*, showing lacune. *l*, lacunes; *r*, root-hairs. × 70.

PLATE 28

a. Transverse section of small root of *Salomonia biflora* (*Polygonatum biflorum*) showing 6-rayed xylem with endodermal layer interrupted opposite the xylem points. Also the great development of water-holding cells in cortex. × 70.

b. Transverse section of a root of *Trichostema dichotomum* in which secondary thickening has taken place. The vessels are large and numerous. No sclerenchyma-cells in the cortex. × 70.

c. Transverse section of secondarily thickened root of *Polygonum Convolvulus*. The vessels are extremely large. A few strengthening cells in the cortex. × 70.

d. Transverse sections of secondarily thickened root of *Crotalaria sagittalis*. The vessels are large and numerous, and sclerenchyma-cells are abundant in the cortex. × 83.